THE METAMORPHOSIS OF SISYRA.

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SISYRA, like most of the Hemerobiidæ, is an insect of whose life history no thorough study has been made, and very little is known of either its habits or metamorphosis. It is an obscure little fly, chiefly interesting on account of some peculiar structures of its larva. The larva has been known since Westwood described it in 1839, but it has never been reared until last summer, at the entomological field station at Saranac Inn, New York. It passes its larval existence as a parasite on fresh-water sponges, clinging to their surfaces or descending into the open osteoles, piercing the sponge tissue with its long decurved jaws. The food thus obtained is so pure as to be wholly absorbed, leaving no residuum. At least one-fourth of the posterior portion of the stomach is atrophied, leaving no opening from the stomach at that end. Carnivorous habits and piercing mouth parts are common to other hemerobian larvæ, but the decurved position of the mouth parts and the tracheal gills are peculiar alone to this insect and Climacia, its nearest ally, which is of similar habits. The singular adaptations of the mouth parts and alimentary tract to the nature of its food I shall describe in detail in this paper.

The most remarkable structure of this larva is the silk-secreting apparatus. In general the silk glands of insects are metamorphosed salivary glands, but in the Sisyra larva they are a modification of the Malpighian tubules; and it seems probable that the nitrogen waste of the body is used, partially at least, in the manufacture of silk. This seems to be another remarkable instance of the economy of the by-product occurring in insect life. No such extensive modification of structure in adaptation to a peculiar environment has been described in any other insect; but two near relatives of Sisyra, Osmylus and Myrmeleon, have a somewhat similar development of silk glands.

The species which I have studied for this paper is *Sisyra umbrata* Needham, and all my specimens were collected for me, a few at Lake Forest and the remainder at Saranac Inn. I have necessarily worked under limitations, not having myself seen any living specimens.

The adult (Fig. 1) is a smoky brown fly, 6–8 mm. long, very hairy, and with the characteristic venation of the Hemerobiidæ, although the wings are not so delicate and transparent as are those of the lacewing flies. The maxilla and labium of the adult, each with peculiar pediform, terminal, palpal joints, are

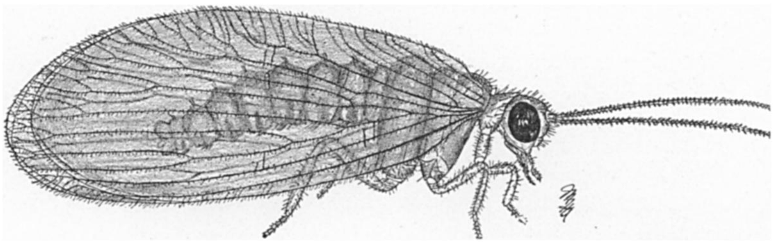

FIG. 1.—*Sisyra umbrata*, adult. × 10.

shown in Fig. 2. Other parts of the imago—antenna, leg, and wing—are figured and discussed later, in comparison with the same parts in the larva.

The pupa, removed from its double cocoon of finely woven silk, is shown in Fig. 3. It is 4 mm. in length, has two clusters of hairs on the dorsal surface of each segment, and is similar to the larva in color and marking, except that the light median line on the dorsal surface between two dark ones, so apparent in the larva, is not visible. Instead the brown crescent-shaped markings on either side meet in a dark median line.

LARVA — EXTERNAL ANATOMY.

The larva (Fig. 4) is 6 mm. in length, is yellowish green in color, and has quite a distinct color pattern in brown on the dorsal surface. Each of the first seven segments bears, in two dorsal and two lateral groups, twelve projections, except the first abdominal, which has only four on the dorsal surface

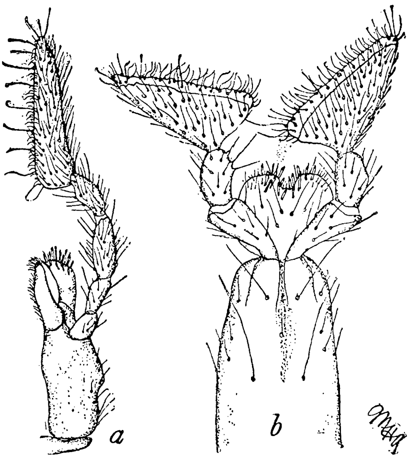

FIG. 2. — Mouth parts of adult. *a*, maxilla, × 60; *b*, labium.

but six on the lateral. Each of these is provided with a long hair. Their purpose seems to be for protection, as the floating particles retained in them make the insect look very much like a diminutive piece of aquatic vegetation. The same thing is described by Kent for Hemerobius, where the protection is furnished by the dead bodies of its victims, the aphids which are held by the long hairs. On the seventh and eighth abdominal segments there is an additional pair of hairs on shorter pedicels, near the median line. On the eighth segment there are two dorsal and two lateral projections, more elongate than those of the other segments, each of which serves as a pedicel for three hairs. The ninth has only the lateral projections. The tenth segment is everted at the end to serve as a spinneret for ejecting the silk. In sections the chitin on this part is noticeably thinner than that covering the rest of the body. Between the head and prothorax on the dorsal side is a small interpolated sclerite, mentioned by Grube, and also by Hagen in his description of Osmylus. There is no trace of it, however, on the ventral side. In Chauliodes, an insect which has the mouth parts normally directed upward rather than downward, as is the case with

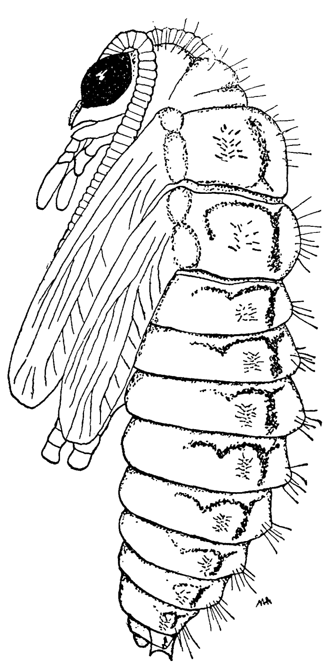

FIG. 3. — *Sisyra umbrata*, pupa. × 21.

Sisyra, there is an interpolated sclerite on the ventral side. The head has on the dorsal surface a pair of hairs directed forward, and on the ventral surface another pair similarly directed but much more elongate.

The larval respiratory apparatus consists of external gills in the form of a pair of jointed appendages on the ventral surface of the first seven abdominal segments, folded under the body so as to be unnoticeable in a dorsal view. They are moved intermittently in a rapid, shuttle-like vibration. Westwood has figured them with five joints, but I have found them uniformly to have only three. The first pair seem to have lost the articulation between the first and second joints. These have thus become two-jointed appendages.

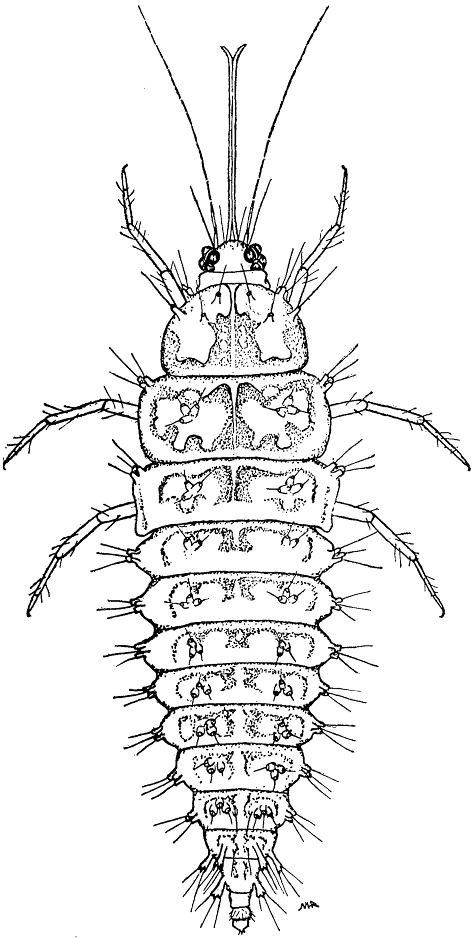

FIG. 4. — *Sisyra umbrata*, larva. × 15.

Near the point of attachment the first pair have a curious hook-like projection (*b*, Fig. 5), directed inward toward the body. This appears on the second pair merely as a knob, and gradually decreases in prominence, until it disappears almost entirely on the sixth and seventh pair (*a*, Fig. 5). On each pair of appendages except the first, at its articulation with the second joint the first one

is forked, the outer branch of the fork being longer than the inner, and both curved inward toward the body. Between these two branches the second joint is attached (*c* and *d*, Fig. 5).

The purpose of these inward-curving forks is probably to keep the respiratory filaments from too close contact with the body, and give them greater access to the currents passing through the pores of the sponge. It would seem that the first pair, having lost the fork at the terminal part of the first joint, have developed the hook-like projection nearer the base for a similar purpose. Two tracheæ can be partially traced in the alcoholic specimens, showing through the delicate outer membrane of the respiratory filaments.

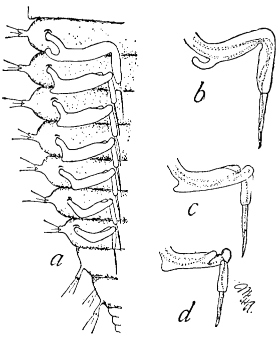

FIG. 5. — Respiratory filaments. *a*, ventral view of abdomen, × 15; *b*, left filament of first pair; *c*, left filament of third pair; *d*, right filament of fifth pair.

The mandibles and maxillæ, to fit them for piercing organs, have attained a length nearly equal to that of the antennæ (Fig. 4) and are joined to form two sucking tubes. In a cross section of these tubes (*a*, Fig. 6) the grooved edges are shown, by means of which mandible and maxilla fit each other closely. The grooved edges of both mandible and maxilla are finely serrated longitudinally, preventing them from slipping one upon another when they are used in puncturing the sponge tissue. The two readily pull apart, showing that there is no adhesion of the chitin, but that they are merely apposed. As seen in Fig. 4, these sucking tubes are conjoined for nearly their entire length, being separated only at the tip and near the base. After they enter the head they unite in a Y-shaped joint, thus forming a single tube. This Y-shaped joint can be plainly seen on the underside of the head in the chitinous shell obtained by the use of caustic potash solution. After the junction the single tube passes on

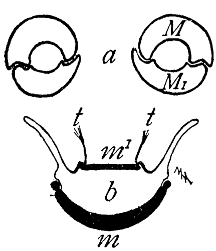

FIG. 6. — *a*, cross section of paired sucking tubes. *M*, mandible; M_1, maxilla; *b*, cross section of pharynx; *t*, tendons; *m*, m^1, points of attachment of muscles.

a nearly vertical line toward the dorsal side, where, after making a turn at right angles, it joins the œsophagus (Fig. 10).

In *b*, Fig. 6, is shown a cross section of the sucking organ (pharynx) after the point of juncture of the two tubes into one. On the anterior and posterior side it is heavily chitinized, these surfaces, together with the tendons on the anterior side, being the points of attachment for two pairs of strong muscle bands. The remaining portion of the wall of this sucking pharynx is of thin membrane. At the contraction of the muscles surrounding it, the cavity within is increased many times the size it has when the muscles are relaxed. This mechanical contrivance forms a very effective pump for drawing the juices of the sponge tissue through the sucking tubes into the œsophagus.

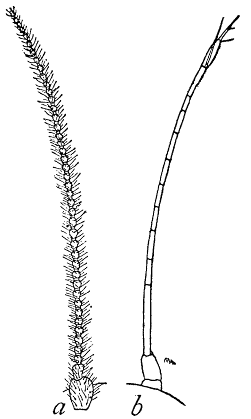

FIG. 7.—Antennæ. *a*, adult, × 18; *b*, larval, × 36.

The larval antenna has in most cases sixteen joints, those beyond the third being usually of equal length. The third is equal in thickness to the segments just mentioned, but equals in length the next three or four segments. The second is equal to the fourth in length, but is twice as thick. The first equals the second in thickness, but is only half as long. The eleventh is frequently somewhat shorter and the twelfth, somewhat longer than the fourth, but they are both equal to it in thickness. The thirteenth is curiously ovate, and the three terminal ones are very slender and bear one or two small spines. At the base of the ovate joint is a much longer spine. In Fig. 7 the antennæ of larva and adult are shown comparatively, but under different magnification.

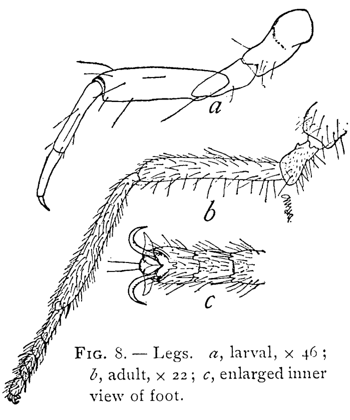

FIG. 8.—Legs. *a*, larval, × 46; *b*, adult, × 22; *c*, enlarged inner view of foot.

Fig. 8 gives a comparative view of the larval and adult leg, and a view of the lower side of the foot of the adult, showing the arrangement of claws and pulvilli, and the four large spines on the inner side of the first four joints of the tarsus. Similar spines occur on the lower end of the tibia. The larval leg has but one claw and a one-jointed tarsus. The legs of the larva are all similar. Those of the adult differ considerably; the fore legs are the shortest pair but have the coxa of unusual length, nearly equal to the tibia; in the middle leg the femur is the longest joint; in the hind leg the femur and tibia are of equal length. In all the adult legs the trochanter is much narrowed at its distal end where it articulates with the coxa.

Before the pupal stage is reached, the legs pull entirely out of their chitinous covering, and the process of making over begins. In specimens lightly stained with borax carmine the adult legs can be distinctly seen developing under the old chitinous covering. This process is shown in Fig. 9, the coxa, trochanter, and femur of the adult leg being fully developed, while the tibia and tarsus with its five joints are only partially differentiated. The process of development for the antennæ and mouth parts of the adult is very similar to that of the legs, except that these adult organs, being so much larger than those of the larva, are early withdrawn entirely out of their slender chitinous sheaths, and are developed underneath the larval cuticle.

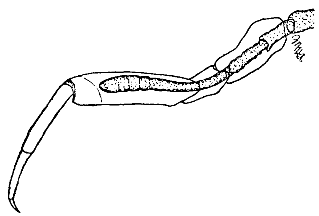

Fig. 9. — Leg transforming.

Internal Anatomy.

Fig. 10 is a diagram of a sagittal section of the larva through the median plane. The position of the brain in the prothorax has been noted in some other insects. In the very young larva the brain occupies the normal position in the head, but, as the pupal stage is approached, it gradually draws backward until it occupies the position in the thorax shown in Fig. 10. The prothorax also contains, besides its own, the subœsophageal

ganglion. The seventh abdominal segment has two ganglia, smaller than those of the prothorax but larger than the remaining eight, which are distributed — one in each of the intervening segments. The dorsal subsegment, interpolated between the prothorax and head, and which was previously mentioned, is shown here. Neither pair of the muscular bands which expand and contract the pharynx (*m*, Fig. 10), nor either of the sucking tubes below their point of juncture (*p*, Fig. 10), would be present in a section through the median plane, but I have figured them here diagrammatically for the sake of clearness.

The most difficult, and, as well, the most interesting part of this study has been the tracing of the course of the alimentary

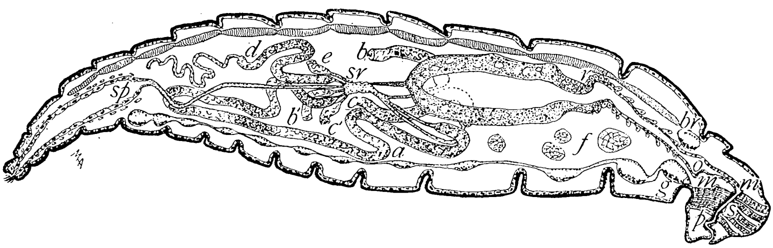

FIG. 10. — General diagram of the larva. *a*, *b–b'*, *c–c'*, three silk glands attached at both ends; *d*, *e*, two silk glands attached at one end; *sr*, silk receptacle; *sp*, spinneret; *f*, fat bodies; *br*, brain; *g*, subœsophageal ganglion; *r*, band of regenerative cells of stomach; *p*, point of junction of sucking tubes; *s*, sucking pharynx; *m*, muscle attachment of pharynx; *o*, œsophagus.

canal posteriorly from the stomach. That others have experienced like difficulties in dealing with near relatives is shown by the contradictory statements made concerning Osmylus by students of its life history (Suckow, Ramdohr, Loew, Dufour, and Hagen). I have found the work particularly difficult, as the alcoholic specimens were too brittle for dissection, and I was obliged to depend entirely upon the study of sections.

Hagen figures for Osmylus four Malpighian tubules attached at both ends to the intestine, the anterior attachment near the base of the stomach, the posterior one near the hinder end of the intestine. Three other tubules have only the anterior attachment and have their posterior end free. All of the tubules are modified in their middle portion for the secretion of silk.

Meinert found similar conditions in Myrmeleon, except that there were six tubes with the double attachment and two with free ends. He also found that there was no posterior exit from the stomach, but that the small intestine (?) had atrophied into a compact string of cells with no opening between the point of attachment of the silk-secreting tubes. The unassimilated portion of residuum is expelled as a mass after the insect has become an imago.

In Sisyra, as I have before mentioned, there is no such residuum, since the juices of the sponge are ready for complete absorption. An extensive digestive tract being in this way rendered superfluous, nature has economized by modifying a large part of the alimentary apparatus into a silk-secreting organ.

The posterior fourth of the stomach appears merely as a solid cord of atrophied cells, which ends in the walls of a dilatation, — "silk receptacle," it may be termed. The walls of this receptacle have the structure of those of the Malpighian tubules. It appears to be the outlet of five tubules, three of which are attached here at both ends, and two of which extend posteriorly and end in the body cavity. All are modified in their middle portions for the secretion of silk. The cells of the silk-secreting portion are much larger and more irregular in shape than the ordinary Malpighian tubule cells, and show the singular branched nuclei characteristic of silk gland cells in the caterpillar and other insects.

The three tubes having the double attachment proceed anteriorly to about the middle of the metathorax and are then modified at or near the point of their backward turn. Posteriorly they are modified almost immediately after leaving the silk receptacle at the base of the stomach. The two tubes having the single attachment have a considerable portion of unmodified tubule at their distal extremity, intricately coiled upon itself, as is shown by the number of variously cut sections which appear at this place in any of the three standard planes through the body. The length of the silk-secreting portion is increased by complicated coils and turns of the tubes, so that they completely fill the body cavity in the first seven abdominal segments, making it next to impossible to accurately trace

their course in sections. It seems probable, however, that there is no constancy in the nature of these coils, as the number of sections of the tubes varies greatly in different specimens. I am reasonably certain, however, of the three attached and two free tubes, as the cross sections show quite uniformly in the anterior portion of the abdomen multiples of three, and in the posterior, multiples of five. The variations from this number can be accounted for by turns in the tubes.

Connecting the silk receptable with the spinneret, which occupies the last three abdominal segments, is a tube which seems to have a straight course except for a bend ventrally in the sixth segment. This is the outlet for the silk secretion which collects first in the silk receptacle. The walls of this outlet tube have somewhat the structure of those of the Malpighian tubules, yet the cells are more regular in shape and have greater uniformity in the size and number of their nuclei. They also show, in a slight degree, the columnar nature of intestinal cells. This fact, together with the ventral bend in the course of the tube and its terminations, indicates that it is the small intestine, entirely diverted from its original function and modified so as to serve merely as an outlet for the silk secretion.

After passing through this tube, the silk collects in the spinneret, the walls of which are surrounded by bands of strong circular muscles, which aid in ejecting the secretion when the cocoon is spun.

In Fig. 10 the nature and position of the spinning glands are shown diagrammatically. The complete course of one of the three which are attached at both ends, and of one of the two which are attached at one end, is figured.

Fig. 11 shows longitudinal and cross sections of the silk glands with their fantastically formed nuclei. The typical structure of the Malpighian tubule is also shown and its gradual modification into silk-secreting cells. In *a*, Fig. 11, a section of a functional silk gland is shown, the walls being much thinner and the nuclei of simpler forms than in *b* of the same figure, where no secretion is visible. Some of the sections figured show traces of vacuolization, a common sign of the

degeneration which is characteristic of the first stage of metamorphosis. Sections of older larvæ show the silk glands in a much more advanced stage of degeneration, and numerous leucocytes in their vicinity or clinging to their walls. In the pupæ there are only a few fragments of the larval silk glands, but adult Malpighian tubules are seen forming, for which the material from the degenerated silk glands is probably again used.

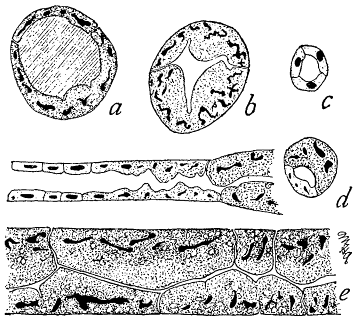

Fig. 11. — Silk gland sections. *a*, cross section of functional gland; *b*, cross section of gland without secretion; *c*, cross section of unmodified tubule; *d*, section showing gradual modification into silk-secreting cells; *e*, longitudinal section of silk gland, showing vacuolization.

Digestive Epithelium. — Sections through the digestive epithelium of a normal, feeding larva show vacuolization, even at this early stage At the anterior end of the stomach is a circular band of small cells which remain active and functional during the period of degeneration of the other epithelium. In the process of degeneration all traces of cell boundaries disappear, in some places the cell substance being a liquid mass in which float the nuclei. The disintegrated epithelium is finally cast off from the walls into the center of the cavity and the new rapidly grows out from the regenerative band to take its place, new nests of regenerative cells appearing at frequent intervals. It would seem that the solid cord of cells at the posterior end of the stomach serves as another regenerative center, since at this stage there is an opening from this end of the stomach through what was the solid cord in the larva. The adult intestine seems to be developing from the cells at this point as a regenerative center. The adult Malpighian tubules are probably also developed in part from these cells. I have seen clear evidences of a new set of these organs forming in the normal position at the base of the stomach.

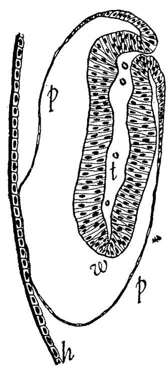

Fig. 12. — Larval wing. *h*, hypodermis; *p*, peripodal membrane; *t*, trachea; *w*, wing.

DEVELOPMENT OF THE WING.

Some time before the larva spins its cocoon the wing buds begin to appear, showing through the thin skin. These form a very convenient index of the age of the larvæ. Fig. 12 represents a longitudinal section through a wing bud at an

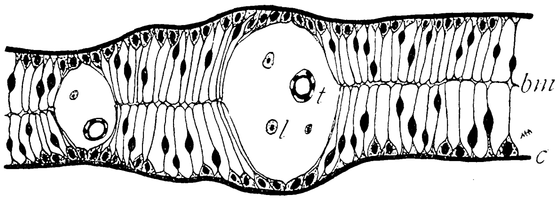

FIG. 13. — Section of older wing. *bm*, basement membrane; *c*, cuticle; *t*, trachea; *l*, leucocytes.

early stage, before it is clearly visible from the outside. The two layers of closely packed cells have not yet united. The first formation of the tracheæ is also shown.

The next stage figured is much later, when the two layers have united, leaving large openings through which pass the tracheæ, now fully developed (Fig. 13). Leucocytes are found frequently in these openings. The great stretching of the wing tissue by its growth both longitudinally and laterally has drawn the upper part of the cells into slender processes, all of

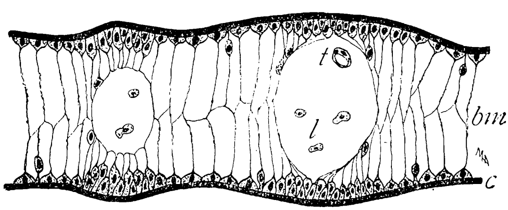

FIG. 14. — Section of older larval wing. *bm*, basement membrane; *c*, cuticle; *t*, trachea; *l*, leucocytes.

which join the basement membrane, separating the two cell layers. Many of the nuclei have been drawn up by the strain from their normal position along the layer of chitin, so that in some cases they nearly touch the basement membrane. The subsequent growth of the wing is nearly all in a longitudinal direction.

Fig. 14 shows the effect of a greater stretching in a longitudinal direction. Most of the nuclei have returned to their position next the cuticle. A very few have progressed too far for return, and are left clinging to the tracheal openings or standing alone and apart from their fellows. The cell processes are much more ragged and broken than in the last stage, and the basement membrane is pulled out of its straight line, being very uneven and irregular. Traces of the old connection may be seen, however, in the slight thickenings in the cell processes. Along the tracheal openings where the adult veins are to be, we see preparation going on for the task of depositing extra layers of chitin. At these points the cells become aggregated in two or more apparent layers and have larger nuclei.

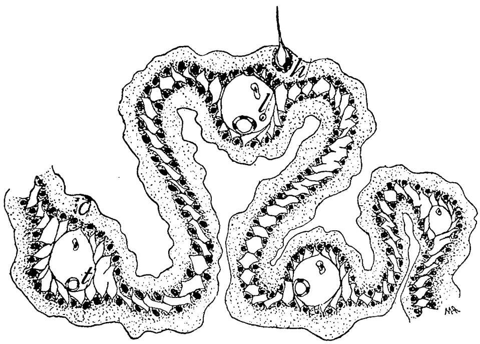

FIG. 15. — Pupal wing. *c*, rudimentary chitin; *h*, mother cell of hair; *l*, leucocytes; *t*, trachea.

The next section figured is from the wing of a pupa (Fig. 15). Here the wing has increased greatly in length and decreased in thickness. The slender cell processes have almost entirely disappeared, all the cells are on one level and have secreted a thick layer of material, which, after the final molt, will harden into chitin. Owing to the close quarters within the pupal skin, the wing has become extensively fluted and crinkled to permit the now rapid growth longitudinally. In Fig. 15 a hair cell is shown developing in the cuticle, — a large vacuolated mother cell, with nucleus at one side and small cells clustered about it.

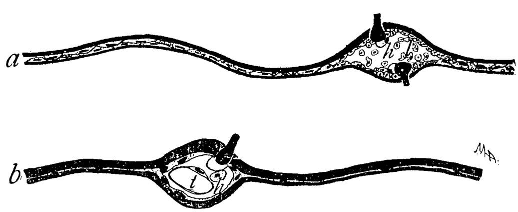

FIG. 16. — Sections of adult wing. *a*, soon after molting; *b*, older. *t*, trachea; *h*, mother cell of hair; *l*, leucocytes.

The next stage shown is from a recently transformed adult (*a*, Fig. 16). The crinkling has disappeared, leaving the wing nearly flat. The processes are contracted within the cell body, drawing the chitinous layers close together. Near the tracheæ are shown the fully developed hair bulbs. The tracheal openings and spaces between the cells show numerous leucocytes, and all the hypodermis is engaged in the work of thickening the chitinous covering.

In *b*, Fig. 16, a section of an older wing is represented. The upper chitinous layer has become much thickened and the only traces of cells are the occasional nuclei and the thin line

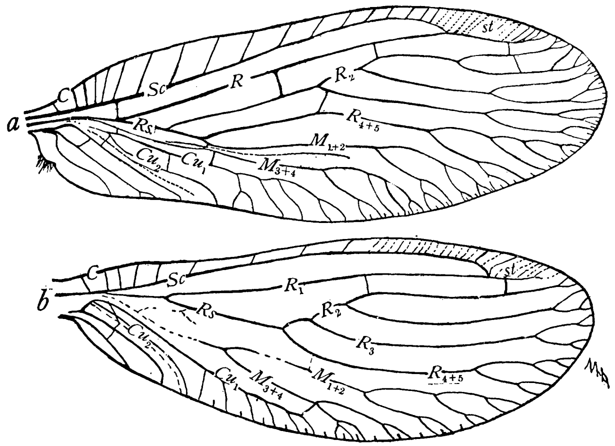

FIG. 17. — Wings of adult, × 15. *a*, fore wing; *b*, hind wing.

of protoplasm between the chitinous layers. In the wings of some insects nothing but the chitinous plates persist, but Sisyra seems to retain throughout this slight vestige of cellular tissue.

Fig. 17 shows the venation of the fore and hind wing of Sisyra. It is rather simple for this family. There are few cross veins. The course of the principal veins may be easily followed. There is, however, quite an extensive variation in the tips of the main branches. A study of this variation should throw some light on the method of evolution of the peculiar hemerobian type. I have tabulated the extent and nature of the variation in fifty wings. Fig. 18 shows the type of branching of the principal

veins, as far out as the point where they cease to be uniform, and the ten different forms of tips appended to these branches, found in the specimens studied. The branches of R_2, R_3, etc., are lettered (*a*, *b*, *c*, etc., Fig. 18), and the different types of tips numbered (1–10, Fig. 18) to correspond with the letters and numbers of the table. The variants and their frequencies are shown for each lettered tip in the table; *e.g.*, tip No. 7 — the most common type — occurs, in the fore wing, four times on branch *a*, sixteen times on branch *b*, etc.

	Fore Wing.										Hind Wing.									
	Left.					Symmetrical.				Right.	Left.					Symmetrical.				Right.
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
a					3		4	14	1	3					2	2	18			3
b					3	2	16			4						5	20			
c						14	11									21	4			
d						5	19			1						23	2			
e					6	2	17									1	24			
f					1		22			2						4	21			
g					1		24								1	11	13			
h						7	18									14	11			
i						12	12	1								22	3			
j						11	13			1						19	6			
k				2	12			9		2					17		1	5		2
l					9		7	5		4					7		13	1		4
m					9		7	5		4					5		20			
n					11		7			7					2		22			1
o				4	16		1	4			2	7	14		2					
p						4	21									25				

From a glance at the table and Fig. 18 one sees the tendency is toward extensive multiplication of symmetrical branches on R_2, and that back of R_5 the branching becomes increasingly asymmetrical toward the left, this asymmetry culminating in Cu_1, especially in the hind wing. No variation in the cross veins of the hind wing was observed in the twenty-five specimens examined, and only a slight variation in those of the fore wing. In every case the variations noticed were in the disk of the wing, except that in two cases there was a cross vein between the first pair of secondary branches of R_2

(*a*, *b*, Fig. 18). Such a case is shown in Fig. 17. The cross vein in the basal part of the subcostal space, said by some to be absent in Sisyra, was present in every specimen. The other variations seen were in the number of cross veins between R_1 and R_2, which is normally three. In two cases four were present and in one other instance there were five. But these were all of a nature easily explainable, as there were two or three faint veins standing close together, showing that the material usually forming one vein had formed several. Between R_2 and R_3, the only other space showing any variation, the

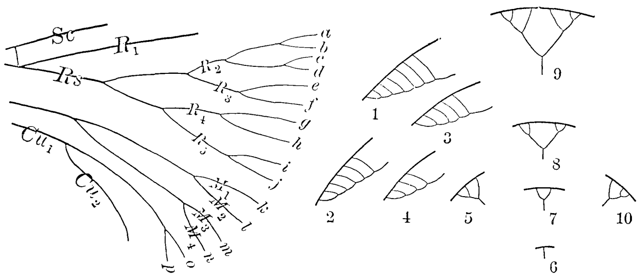

FIG. 18. — Diagram of variation in wing veins, illustrating the table.

normal number is one. In seven cases there were two, in one three, and in one four. The same tendency to have several weak veins close together was shown here. All the added cross veins were on the proximal side of the normal one. The variation in cross veins seems to have no connection with that in the tips. The specimen having the most erratic form of tip (9, Fig. 18), which occurred only once, had the cross veins entirely normal.

SUMMARY.

The points of chief interest developing from this study may be summarized as follows :

1. In Sisyra the mouth parts are not in the usual opposed position, but are approximated in pairs to form two sucking tubes, excessively elongated, and decurved.
2. The brain is in the prothorax in old larvæ.
3. The stomach has no posterior opening in the larva.

4. Three Malpighian tubules are attached at both ends, and two are attached at one end, — all metamorphosed into silk glands in their middle portion.

5. The small intestine is modified into an outlet for the silk secretion.

6. The spinneret is formed from the terminal part of the alimentary canal.

7. A completer account than has hitherto appeared is here given of the late stages of wing development, and the variations in venation of fifty wings are tabulated.

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